PROC. ENTOMOL. SOC. WASH.
89(3), 1987, pp. 532–547

CHIROSIA BETULETI (RINGDAHL) (DIPTERA: ANTHOMYIIDAE) A GALL-FORMER ON THE OSTRICH FERN, *MATTEUCCIA STRUTHIOPTERIS,* WITH NOTES ON OTHER INSECT-FERN ASSOCIATES

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Abstract.—Larvae of *Chirosia betuleti* cause the formation of cover galls in the vegetative leaves of the ostrich fern, *Matteuccia struthiopteris.* This is the first record of this anthomyiid fly in North America. Females lay their eggs on the unfurling fronds. Newly emerged fly larvae feed on glandular hairs causing the pinnules to curl around the midrib, and partially or completely loop around the feeding larvae. Fly eggs and larvae have been found contaminating the fiddleheads of this edible fern. Larvae were parasitized by braconid wasps of the genus *Aphaereta* and eulophid wasps of the genera *Dimmockia* and *Elachertus.* Larvae of the chloropid fly, *Elachiptera costata,* were secondary invaders of the vacated galls. Larvae of *Chirosia betuleti* and *Elachiptera costata* are described in detail for the first time. Effects of the gall on leaf growth are outlined, and the distribution of the galls in a sampled population is described. A cursory description of a gall caused by the tortricid moth, *Olethreutes auricapitana,* is given, and a list of the primary insects collected and identified from the fern is also provided.

Species of the anthomyiid genus *Chirosia* Rondani have been reared from several fern species. Most descriptions of the life cycles of these flies and their effect on the host plant are from the bracken fern, *Pteridium aquilinum* (L.) Kuhn (Meijere, 1911; Cameron, 1930; Meikle, 1937; Brown and McGavin, 1982). *Chirosia betuleti* (Ringdahl) is known from the fern genera *Pteridium* and *Athyrium* in Europe (Meijere, 1911; Seidel, 1957) but has not been recorded previously from *Matteuccia* nor from North America.

Matteuccia struthiopteris (L.) Todaro, the ostrich fern, is found along flood plains in the Northern Hemisphere, where it develops large clonal populations. *Chirosia betuleti* is closely associated with this fern species in eastern Canada, and it is the nature of this association, as well as the effect it has on the fern plant and population, which we describe in this paper. We also describe the unique immature stages of this fly species. During the course of this investigation, a number of other insects were collected from *Matteuccia struthiopteris* or in association with vacated galls. Principal among these was the chloropid fly, *Elachiptera costata* (Loew), whose larva also is described below. A list of the other primary insects collected from the fern during this study is also provided.

Material and Methods

Field collections.—Galls from the ostrich fern were collected initially in June, 1981, from plants growing along Five Mile River, near South Maitland, Hants County, Nova Scotia. In July of the same year, galls were taken into the laboratory and placed in perforated plastic bags. The flies that emerged from these galls were mounted and identified. In the following years, galls were again collected from the same site, as well as from four other locations: Lattie's Brook, River Herbert, and Meander River, all in Hants County, as well as at Cape Split, Kings County, Nova Scotia. Crowns of the fern were collected in late summer and in early autumn of 1983 and taken to the laboratory for dissection.

In 1984, collections were made weekly on the Five Mile River site, beginning May 29, until the first frost in mid-September. In addition, plants were assessed in surveyed transects for a number of leaf characteristics and gall information. Plants were measured in a stand of ferns divided into transects 20 m in length. Each week a transect was chosen and plants selected at 1 m intervals. Leaf dry weight, leaf type, extension and number were measured, and the presence or absence of galls noted. Details on leaf sampling are recorded elsewhere (Aderkas and Green, 1986).

In 1985, a larval collection was made June 16, from the Five Mile River site. The larvae were kept in Sterilite® jars on filter paper moistened with 0.5% Javex® in distilled deionized water. Pupae, which developed by July 16, were maintained in the same way as the larvae and kept at 4°C until November, after which time, at monthly intervals, samples were removed and held at 20°C. In this way three males and a female were recovered.

In addition, information on the occurrence and effect of galls on leaf development was collected from plants removed from a tagged population on the Five Mile River site. These excavated rhizomes and leaves were frozen until examined. The details on leaf characteristics, most of which are not relevant to this study, will be presented elsewhere. During the course of pulling apart these ferns and looking at various morphological features, two puparia were found between leaf bases of different rhizomes.

Preparation of specimens.—All immature stages of the flies were preserved in 70% ethanol for further processing. Specimens for scanning electron microscope study were removed from the ethanol preservative, freeze dried, and glued to the observation stub. Plant specimens were hand sectioned with a straight razor and stained with 0.5% Toluidine Blue 0 in 1% borate (aqueous). Sections of affected and unaffected tissue were viewed under a Leitz Dialux 20 microscope.

Results

Insect phenology and effects on leaf development.—Eggs of *Chirosia betuleti* were laid in early May on the inside of leaflets, on the unfurling portion of the coiled vegetative leaf. They adhered to the sticky hairs, present at this time, on the midrib. Emerging larvae fed on the numerous glandular trichomes in the upper quarter of the groove of the frond rachis. Feeding caused a localized reaction in the expanding frond such that the young leaflets in the immediate vicinity remained stunted, and curled over the midrib (Fig. 28).

In most fronds there were further developments. Along that portion of the midrib on which the larva(e) fed, there was a subsequent partial or, less commonly, a complete loop of the rachis. Often, only a three-quarter twist was completed such that the resulting gall was a sack-like or U-shaped alteration of the normal course of the midrib. In all galls, the larvae were covered by the pinnules (Fig. 27). The portion of the leaf anterior to the feeding larvae continued to develop normally (Fig. 28). At maturity, the leaf was normal in overall shape and size, except for the affected portion which appeared as a looped whorl of pinnules.

In some plants, leaves were found in which the upper pinnules completely failed to unfurl but were kept rolled together over a feeding larva (Fig. 28, O). These pinnules died and fell off, leaving a truncated frond. This condition was found to be caused by the larva of the lepidopteran *Olethreutes auricapitana* (Walsingham) (Tortricidae).

Only one gall was formed per leaf and only rarely was the gall occupied by more than a single larva of *Chirosia betuleti*. Larvae that had eaten most of the trichomes of the rachis continued along the covering pinnules, as well as feeding on epidermal and collenchymatous hypodermal tissues along the adaxial side of the rachis. There was no expansion or other deformation of the midrib. Midribs were never mined since feeding of the larva was restricted to the adaxial surface of the rachis. With continued feeding these areas became black from the accumulation of frass and the enzymatic and bacterial breakdown of the epidermal and hypodermal tissues.

Matteuccia struthiopteris sporophytes initially produced vegetative leaves, followed six weeks after by fertile fronds and cataphylls. In terms of leaf types, galls were found on vegetative fronds, the only leaf type present at the time the eggs of *Chirosia betuleti* were being laid.

Three larval instars were present through May and June. First instar larvae were collected from the middle of May until the first week in June, second instar larvae were present from early June until the beginning of July, and mature larvae were found from mid-June until mid-July. Puparia, which developed from as early as mid-June until mid-July, dropped out of the galls to the soil surface or, occasionally, between leaf bases of the fern rhizome, where they remained over autumn and winter. In the laboratory, larvae were maintained for rearing to pupae, but they did not undergo any further development over the summer. About 20% of the larvae of *C. betuleti* were heavily parasitized by an undescribed braconid wasp closely related to *Aphaereta pallipes* (Say) which is a common, widespread, polyphagous species parasitizing a number of anthomyiid and other muscoid flies. The new wasp will be described by Robert A. Wharton, Texas A&M University, College Station, Texas. These wasps were found in the larvae only after mid-June and prevented the pupae from completing their development to the adult stages. The wasps did not require a cold period prior to emergence, though they might occasionally overwinter within the host as determined from pupae studied in the laboratory. A single female of a species of the eulophid wasp, *Dimmockia* Ashmead, was found in a container with parasitized and non-parasitized pupae being reared to adults, and four males and six females of *Elachertus loh* Schauff (described as new with the holotype female from our material) were also found. Schauff (1985) cited the host of the latter species simply as a leafroller and stated that the specimens from Nova Scotia were reared on ferns.

Of 320 fern plants sampled in the weekly transects, 114 plants had insect galls on their leaves. Plants with galls also had significantly ($P < 0.01$: t. test) more vegetative leaves ($\bar{x} \pm SE = 6.5 \pm 1.0$) than plants without galls (5.2 ± 0.8). Fewer plants than expected had one or two galls and many more plants than expected had three or more galls. Test of fitness (G test) showed that the number of galls per plant did not follow a Poisson distribution, but indicated a clumping of galls. Among plants with galls, there was an average of 2.4 ± 1.3 galls per plant. Occasionally, plants were observed with all leaves inhabited; in one instance, eight galls per eight leaves were found. The highest number of galls found was nine in a plant that possessed 13 leaves. Plants with galls did not necessarily have shorter average leaf lengths (galled leaves—79.0 ± 22.0 mm; unaffected leaves—81.0 ± 14 mm). The presence of the fly larvae distorted the expansion of the pinnae about the gall, but not the overall height expansion of the leaf.

At the Cape Split site, galls were observed on two plants of *Dryopteris carthusiana* (Villars) Fuchs, but the absence of larvae at the time of observation (late June) precluded positive identification of the gall former. However, the peculiar damage indicates that a species of *Chirosia* probably was responsible for these galls as well.

Infestation differed from one year to the next. In 1984, 36% of the fern plants were affected, but in 1985, only 30% were affected. Of the originally affected plants, 60% were infected two years in a row.

In the latter part of June, pupae of *Chirosia betuleti* were falling to the ground when females of the chloropid fly, *Elachiptera costata* (Loew) laid their eggs in the vacant cover galls. Generally, only one chloropid larva inhabited each gall, but sometimes two were found, and as many as ten were counted jointly inhabiting one gall. Larvae fed on superficial plant tissue within the gall and pupated by mid-July; adults emerged at the end of July and the beginning of August. No parasites were found associated with the immatures of this species.

In the course of one year, *E. costata* completed two generations. Second generation larvae inhabited late developing leaves (cataphylls) nearest the crown, destroying the young leaf tissue, and overwintered in the debris. Eggs were laid on or under the moist papery scales that covered the emergent cataphylls, and larvae burrowed among these scales until they reached the pinnules of the crozier. From observations on feeding larvae, it was apparent that trichomes were the food of choice, and when most of these had been consumed, the cataphyllar leaf tissue was eaten. The damage to the young fronds was extensive, always resulting in death of the organ. On an affected crown, which produces an average of two cataphylls per year, all cataphylls may be affected. The larvae of *E. costata* overwintered under the papery scales, pupated with the onset of warmer weather, and emerged as adults by early June.

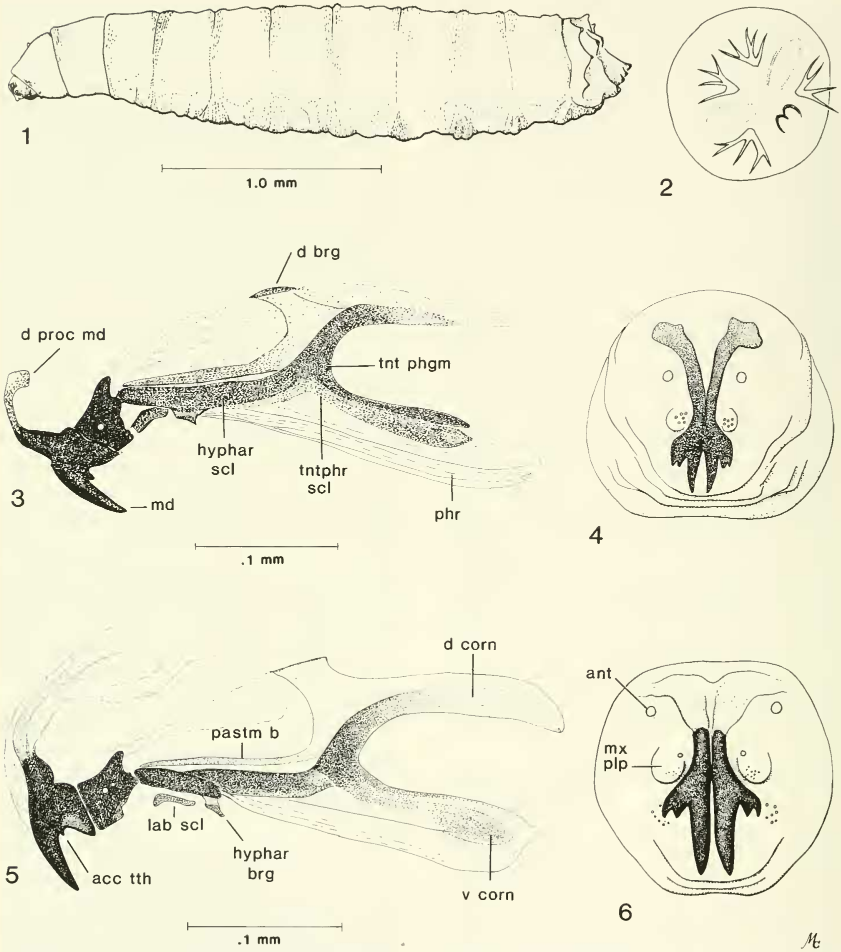
Descriptions of Immature Stages

Chirosia betuleti (Ringdahl)

Egg.—Pale white; elongate cylindrical, tapering to a rounded apex at anterior end, broadly truncate at posterior end (Figs. 13–15); length 1.44–1.69 mm. Chorionic membrane with a markedly reticulate sculpturing.

First instar larva (Figs. 1–4, 16–18).—Pale yellowish white; slender, subcylindrical, tapering anteriorly, rounded posteriorly; 0.90–1.61 (av 1.18) mm long on hatching, growing to about 2.82 mm before moulting to second instar. Integument without any apparent pattern or ornamentation except for ventral surface and anterolateral margins of abdominal segments 1–7, that are somewhat wrinkled; creeping welts and anterior margins of these segments bearing narrow rows of minute spinules, these spinules more numerous on creeping welts than on dorsum of abdominal segments; a few spinules also present ventrally on anterior margins of thoracic segments 2 and 3, and on terminal abdominal segment where they are more numerous. Terminal segment with eight short tubercles, four dorsal and four ventral to posterior spiracles. Perianal pad relatively large, well-defined, each lateral half subdivided into a smaller anterior lobe and a slightly larger posterior lobe. Anterior spiracles absent. Posterior spiracles situated on short, cylindrical and subparallel stigmatophores, each spiracular plate bearing two small, weakly defined but distinctly separated openings that have faintly sclerotized but incomplete margins, and a somewhat W-shaped or cordate sclerite with a heavily sclerotized, incomplete margin (Fig. 2).

Cephalopharyngeal skeleton (Fig. 3) slender, seemingly delicate even though rather heavily sclerotized. Mandible relatively long, slender, pointed, with a single tiny accessory

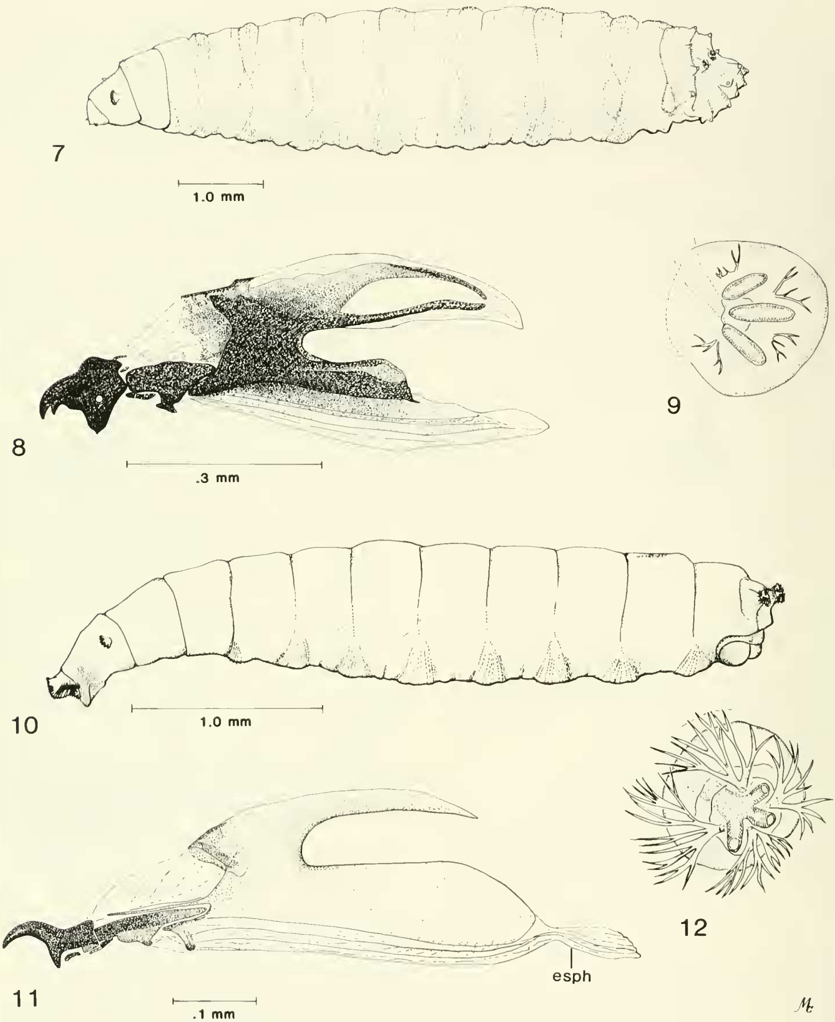


Figs. 1–6. *Chirosia betuleti,* larva. 1, Habitus, first instar. 2, Posterior spiracular plate, first instar. 3, Left lateral view of cephalopharyngeal skeleton, first instar. 4, Anterior (end on) view of head segment showing mouth hooks and their dorsal sclerotized processes, first instar. 5, Left lateral view of cephalopharyngeal skeleton, second instar. 6, Anterior (end on) view of head segment showing mouth hooks, second instar. Abbreviations: acc tth, accessory tooth; ant, antenna; d brg, dorsal bridge; d corn, dorsal cornu; d proc md, dorsal process of mandible; hyphar brg, ventral bridge of hypopharyngeal sclerite; hyphar scl, hypopharyngeal sclerite; lab scl, labial sclerite; md, mandible; mx plp, maxillary palpus; pastm b, parastomal bar; phr, pharynx; tnt phgm, tentorial phragma; tntphr scl, tentoropharyngeal sclerite; v corn, ventral cornu.

tooth on ventral margin, and two (occasionally three) prominent teeth on outside margin; also bearing a slender, heavily sclerotized, antler-like process that extends dorsally along medial margin of antennomaxillary lobe and curves laterally and expands plate-like dorsally over antenna and maxilla (Fig. 4); this process intimately connected with integument and not free from or external to it. Hypopharyngeal sclerite relatively long, moderately stout. Dental sclerite absent. Labial sclerite small, slender, but well-developed and heavily sclerotized. Parastomal bar long, moderately stout and rather heavily sclerotized. Tentoropharyngeal sclerite with tentorial phragma short, dorsal cornu nearly horizontal, distinctly longer and more slender than ventral cornu but becoming weaker and pointed posteriorly; ventral cornu relatively stout and rather bluntly rounded posteriorly, with a slender clear band posteriorly below dorsal margin; ventral cornu occasionally strongly angled posteroventrally in relation to dorsal cornu (this angle seemingly decreases as the larva increases in size approaching moult to second instar). Dorsal bridge prominent, elevated slightly above dorsal cornu, only moderately sclerotized.

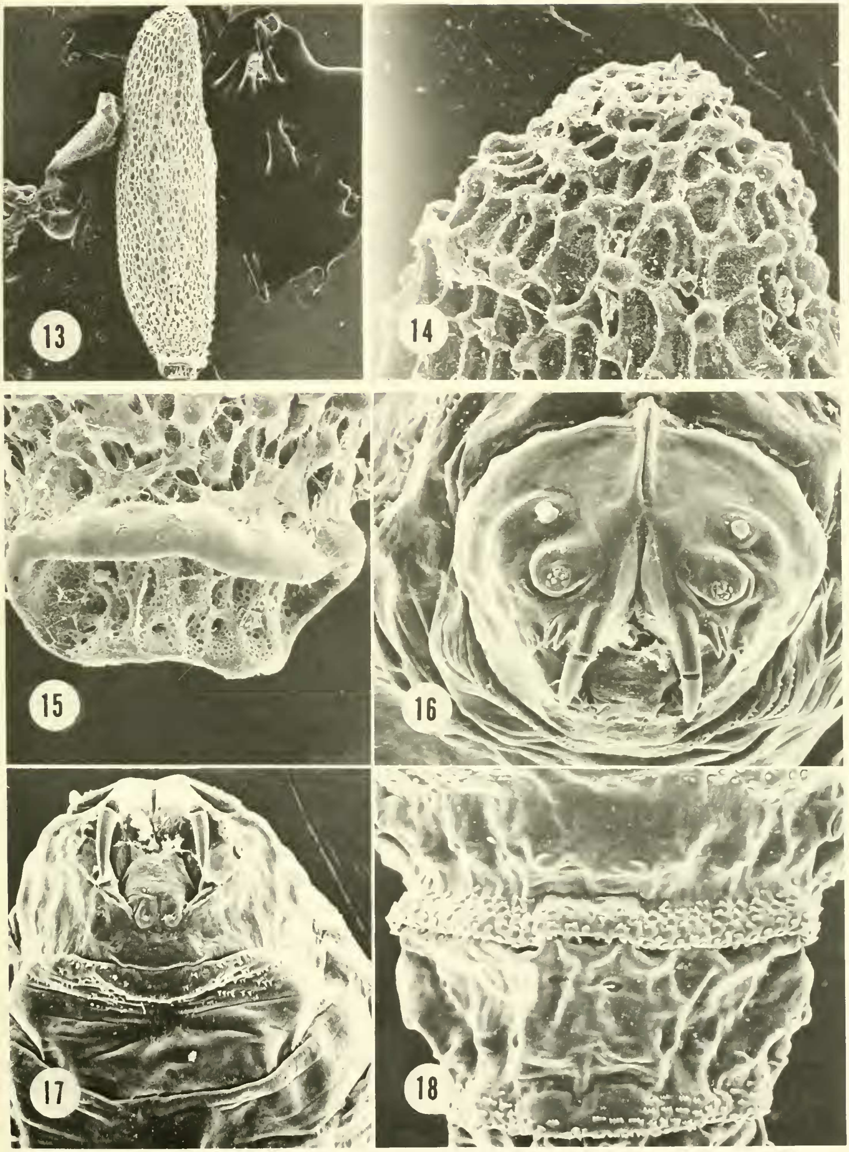
Mature larva (Figs. 7–9, 19–26).—Pale yellowish white; subcylindrical, tapering anteriorly, broadly rounded posteriorly; length 4.08–8.76 (av 7.25) mm; greatest width 0.85–1.92 (av 1.60) mm. Integument mostly smooth except along anterior margins of segments both dorsally and ventrally. Creeping welts small, covered with a moderately dense concentration of minute, slightly raised, spiniform integumental processes that often are difficult to see; these processes extending dorsally along anterolateral margin of each abdominal segment forming a continuous narrow band that expands dorsally so that each segment has a more or less distinct collar or girdle anteriorly. Antennomaxillary lobe of cephalic segment with a small, single segmented, somewhat dome-shaped antenna; maxilla distinct, with about five sensory areas; and with about 15–17 oral ridges. Terminal segment with integument slightly granulate, and bearing a series of 16 small but conspicuous tubercles, each with a central pore, arranged as follows: six dorsal tubercles situated in front of posterior spiracles in a nearly transverse row that is broken medially (two submedian, two sublateral, two lateral); six tubercles with a similar arrangement behind posterior spiracles; two slightly more ventrally placed submedian tubercles; and two submedian ventral tubercles dorsal to anus (Fig. 25); area between these two ventral tubercles and anus with a patch of 10–30 dark spinules. Perianal pad moderately large, oval, well-defined, anus situated longitudinally. Anterior spiracle (Figs. 7, 23, 24) somewhat flattened and fan-like with about 21 minute papillae arranged in a slightly irregular row. Posterior spiracles (Figs. 9, 25) situated on two slightly elevated cylindrical stigmataphores; each spiracular plate bearing three oval openings set at about a 20° angle to nearest opening, each opening surrounded by a narrow partially sclerotized ring; with four spiracular hairs that are small but visible with a dissecting microscope, palmate with 4–10 (rarely more) branches that are mostly bifurcate near tips but with some simple branches; peritreme weakly sclerotized, incomplete. Ecdysial scar not evident.

Cephalopharyngeal skeleton rather robust, heavily sclerotized but tentoropharyngeal sclerite mottled by paler and less densely sclerotized areas (Fig. 8). Mandible short, stout, with one or two variably stout accessory teeth on ventral margin. Hypopharyngeal sclerite relatively large, stout; hypopharyngeal bridge bowed ventrally so that in lateral view, it projects conspicuously below lateral arms of this sclerite. Dorsal and ventral labial sclerites U-shaped, rather weakly sclerotized, often somewhat nebulous and irregular in structure. Parastomal



Figs. 7–12. 7–9. *Chirosia betuleti,* third instar larva. 7, Habitus. 8, Left lateral view of cephalopharyngeal skeleton. 9, Posterior spiracular plate. 10–12. *Elachiptera costata,* third instar larva. 10, Habitus. 11, Left lateral view of cephalopharyngeal skeleton. 12, Posterior spiracular plate. Abbreviation: esph, esophagus.

bar apparently absent. Tentoropharyngeal sclerite stout; tentorial phragmata relatively long, it and ventral cornu dark, heavily sclerotized except entire ventral margin and at least posterior ½ of dorsal margin of ventral cornu more weakly sclerotized and paler brownish; dorsal cornu broad, weakly sclerotized except heavily and narrowly sclero-



Figs. 13–18. Scanning electronmicrographs of *Chirosia betuleti.* 13, Egg. 14, Anterior portion of egg. 15, Posterior portion of egg. 16, Head, first instar larva. 17, Ventral aspect of head of first instar larva showing labial palpi. 18, Dorsal integumental armature of segmental collar of first instar larva.

tized along ventral margin, posterior ⅓ to ⅔ of dorsal cornu with a clear, unsclerotized 'window.' Dorsal bridge broad, prominent, but rather weakly sclerotized, mottled with clear, roundish spots.

Puparium.—Dark yellowish to reddish brown; length 4.38–6.37 (av 5.27) mm, width 1.26–2.21 (av 1.72) mm. Somewhat barrel-shaped and showing gross external features of mature larva. First two thoracic segments somewhat flattened, metathoracic segment slightly smaller than abdominal segments; anterior segment subtruncate, weakly emarginate medially, and bearing anterior spiracles at each anterolateral corner.

Comments.—The specific identity of this anthomyiid fly seems reasonably certain despite the paucity of good adult specimens. F. C. Thompson, Systematic Entomology Laboratory, Washington, D.C., compared the male terminalia of our specimens with those of a European specimen of *C. betuleti* housed in the U.S. National Museum collection, and found them to match very closely. This identification was subsequently confirmed by V. Michelsen, Zoological Museum, Copenhagen, Denmark, who also kindly compared our one good specimen with European material. In his treatment of the Palearctic anthomyiids, Hennig (1966) indicated that the life history and larval descriptions given under the name *Chortophila signata* Brischke by Meijere (1911) really applied to *Chirosia betuleti*. An examination of Meijere's figures (plate 6, figures 16–19) shows that they are similar to our specimens. However, the anterior spiracle and the mandible of Meijere's figures show just enough differences from our material to support the possibility that there really are two species. On the other hand, it is possible that Meijere's figures are not as accurate as they could be and thus may be of little comparative value in helping resolve our species identification problem. In any event, we are calling our species *Chirosia betuleti* until additional comparative material of all stages, from both Europe and North America, is available to enable us to revise this identification if necessary. Our specimens represent the first record of this species in North America. Huckett (1965) recorded only two species of *Chirosia* from North America, viz. *C. hirtipes* Stein, a Holarctic species, and *C. idahensis* Stein, a western U.S. species. In 1974, he listed four additional species from North America: *C. delicata* (Huckett), *C. pusillans* (Huckett), and *C. stratifrons* (Huckett) all from eastern U.S., and *C. hystrix* (Brischke) (= *C. hystricina* Rondani) a Holarctic species.

From the many larvae of *C. betuleti* that pupated, only five females and four males emerged. Of these, only three females and one male were good specimens; the other adults were damaged during emergence. Most of the larvae that pupated were heavily parasitized by the undescribed braconid wasp mentioned earlier, which prevented further development of the flies.

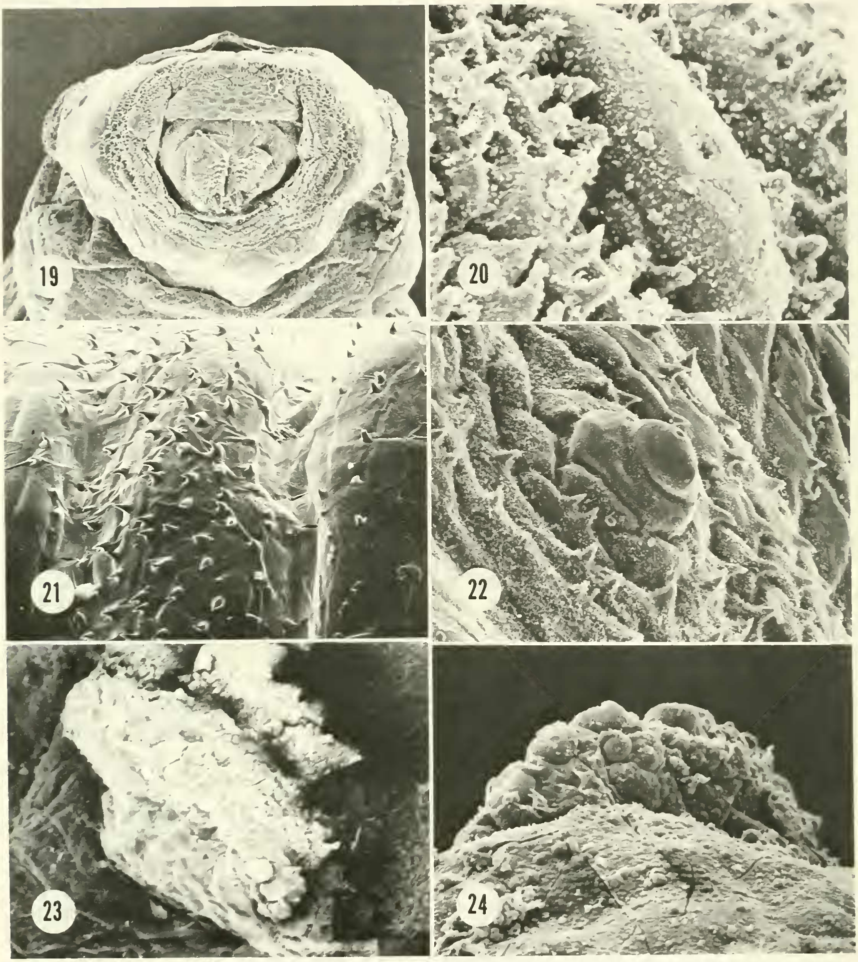
The above descriptions were based upon the examination of 42 eggs, 62 first instar larvae, 28 second instar larvae, 122 third instar larvae, and 21 puparia of which nine were associated with the reared adults mentioned above.

The first instar larva closely resembles the second and third instar larvae in general appearance. However, apart from size, some interesting changes in certain morphological features are dramatically evident between the three larval stages. Externally, the terminal segment of the first instar larva seems to bear only eight tiny posterior lobes, four dorsal and four ventral to the posterior spiracles. In the third instar larva 16 lobes are evident although these are not all the same size. Possibly all 16 lobes are present in the first instar larva but some may be so small they are extremely difficult to discern. Also, the posterior spiracle of the first instar larva has only two incompletely defined spiracular openings and a well-defined sclerite that has a heavily sclerotized but incomplete cordate margin. Each spiracle of the mature larva has three openings and the ecdysial scar is not evident. As in at least some of the first instar larvae of the Muscoidea, the anterior spiracle is absent. In the second instar larva the anterior spiracle is present but small and sometimes difficult to see, especially in recently moulted specimens. This spiracle in the third instar larva is well-developed and prominent. Anteriorly, the most notable and visible difference in the first instar larva is the presence of a sclerotized antler-like process extending dorsally from the top of each mandible. This process is darkly pigmented and extends above and over the antenna where it expands plate-like laterally. The origin and function of these structures is not known. They might be remnants of some ancestral structures, and possibly might be used in breaking out of the egg. In the second instar larva only a short remnant of this process remains; however, visible traces of the position it occupied in the first instar larva remain in the cuticle of the second instar larva (Figs. 5, 6). All traces of this antler-like process are absent in the third instar larva. The mandibles of the first and second instar larvae are long and slender whereas the mandible of the third instar larva is short and stout. In the first two instars there is a roughly quadrate sclerite, bearing a tiny but distinct aperture, that is directly behind and clearly separated from the mandible. In the mature larva this sclerite is fused with the mandible proper. It is interesting that the cephalopharyngeal skeletons of the first two instar larvae are quite similar except for the difference in size. Normally, the cephalopharyngeal skeleton of the second instar larva more closely resembles that of the third instar larva than it does the cephalopharyngeal skeleton of the first instar larva. The hypopharyngeal sclerite in the first instar larva is stout and apparently fused with the tentopharyngeal sclerite, and the parastomal bar is moderately broad and sclerotized. In the second instar larva there is a distinct line of demarcation between the hypopharyngeal and tentoropharyngeal sclerites, yet they remain heavily sclerotized, while the parastomal bar is somewhat more slender and less sclerotized. In the third instar larva the hypopharyngeal sclerite is shortened but still strongly sclerotized, the anteroventral marginal process of the tentoropharyngeal sclerite is much shorter, the tentoropharyngeal phragma is much longer, the dorsal and ventral cornua are stouter and the dorsal cornu has a distinct window-like area posteriorly. Also, the parastomal bar apparently has disappeared in the mature larva. Other progressive changes can be seen in Figures 2–9. Without having representatives of associated larvae of each instar it would be easy to suspect the three morphological forms of the larvae of this species as representing three distinct species.

The only other anthomyiid first instar larva presently known to the authors that possesses similar antler-like processes extending dorsally from the mandibles is that of *Macateeia protuberans* Malloch. However, there are some marked differences between the processes, as well as between the entire cephalopharyngeal skeletons of these two species. Karl Valley, Pennsylvania Department of Agriculture, Harrisburg, Pennsylvania, who brought the first instar larva of this species to our attention, plans to describe it in detail. In *M. protuberans* this antler-like process is shorter, broader, less sclerotized and brownish over most of its length, and the plate-like expansion over the antenna is larger, more weakly sclerotized and less discrete than in *Chirosia betuleti*. Again, the function of this structure is not known. This process may be more commonly present among the first instar larvae of phytophagous anthomyiid flies than is currently known.

Elachiptera costata (Loew)

Mature larva (Figs. 10–12).—Creamy white; subcylindrical, tapering anteriorly, broadly rounded posteriorly. Length 3.18–



Figs. 19–24. Scanning electronmicrographs of *Chirosia betuleti,* third instar larva. 19, Anterior view of head (partly withdrawn) and anterior thoracic segment showing armature. 20, Close-up of thoracic armature and pore. 21, Dorsal integumental armature of segmental collar of abdomen. 22, Close-up of integumental armature of collar and pore of posterior abdominal segment. 23, Anterior spiracle, dorsal view. 24, Anterior spiracle, lateral view.

3.64 (av 3.35) mm; width 0.46–0.65 (av 0.58) mm. Integument smooth except for small creeping welts that are beset with 5–7 irregular rows of spinules; these spinules are minute but those of third posteriormost row are largest and those of second anteriormost row are next to largest; spinules on abdominal segments 1–7 extending dorsally about ¼ to ½ height of segments. Antennomaxillary lobe of cephalic segment with a small but prominent 2-segmented antenna having a pair of basiconic sensillae at junction of the two segments, an inconspicuous maxilla, and about 15 oral ridges. Terminal segment smooth, without accessory tubercles, but ventrally with a small, well-developed, transversely oval perianal pad that is divided into four subequal lobes; and dorsally bearing posterior spiracles on two short cylindrical stigmatophores (Fig. 10). Each spiracular plate (Fig. 12) with three small, round openings, the lateral openings set at about 30° to 40° from central opening; each opening with a slightly thickened and lightly sclerotized rim; all three openings encircled by a lightly sclerotized, somewhat poorly defined peritreme; with four conspicuous multibranched spiracular hairs; ecdysial scar not apparent. Anterior spiracle small, fan-like, with six minute papillae.

Cephalopharyngeal skeleton (Fig. 11) well-developed and moderately robust; mandible and hypopharyngeal sclerite heavily sclerotized, tentoropharyngeal sclerite rather lightly sclerotized except heavily sclerotized along anterior rim of dorsal bridge and along ventral margin of dorsal cornu and continuing ventrally along hind margin of tentorial phragma. Mandible rather long, slender, decurved, and with a prominent, ventral, pointed process. Hypopharyngeal sclerite stout, with a broad hypopharyngeal bridge. Dental sclerite small, somewhat crescent to triangular in shape; labial sclerite slender, U- to V-shaped with the two sides not fused or weakly joined anteromedially; parastomal bar long, slender and weakly to moderately sclerotized. Dorsal bridge prominent; dorsal cornu shorter than ventral cornu, slender and pointed posteriorly; ventral cornu broad, rounded posteriorly and lightly sclerotized.

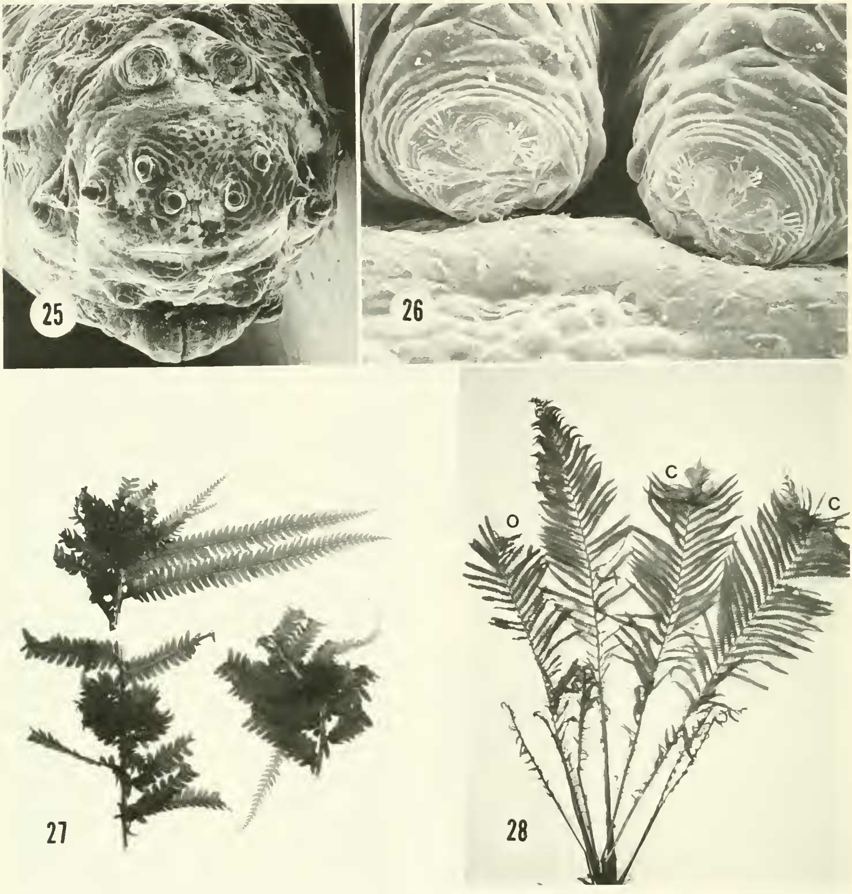
First and second instar larvae externally similar to mature larva, but first instar larva ranging from 0.37–0.60 mm in length, and the second instar larva ranging from 1.05–2.8 mm in length.

Puparium.—Brownish yellow; length 2.28–3.22 (av 2.57) mm; width 0.60–0.93 (av 0.72) mm. External features essentially as in mature larva except anterior two (thoracic) segments broadly flattened; anterior margin truncate, with a shallow median notch, and bearing anterior spiracles at each anterolateral corner.

Comments.—The above descriptions of *E. costata* were based on the examination of three mature larvae, and 24 puparia (seven puparia were associated with reared adults). Also available were 11 first instar larvae, two second instar larvae, and 71 reared adults without associated puparia. The above larval and pupal descriptions apparently are the first for this species.

Discussion

Chirosia is a genus intimately associated with ferns. Of the 14 Palearctic species (Wiezorek, 1973), the nine species for which any hosts are known occur exclusively on ferns. These anthomyiids are either leaf rollers, leaf miners, or gall formers. Six species (*C. albifrons* Tiensuu, *C. albitarsis* Zetterstedt, *C. betuleti, C. crassiseta* Stein, *C. hystericina* Rondani, and *C. parvicornis* Zetterstedt) have had their life cycles described (Wiezorek, 1973; Brown and McGavin, 1982), but the life cycles of the other species are poorly known or undescribed. The life cycle of *Chirosia betuleti* has been described by Meijere (1911) and Seidel (1957), and our observations broadly concur with their descriptions. *Chirosia betuleti* is not restricted to one species of fern. Meijere (1911) records it from *Pteridium aquilinum* as well as on *Athyrium*. Our report of this fly on the genus *Matteuccia* means that it is oligophagous, restricting itself to a few fern genera. Most gall formers are monophagous (Gerson, 1979). Several species of *Chirosia* (e.g. *C. albitarsis, C. albifrons, C. crassiseta*) have been reported only from bracken (Cameron, 1930; Meikle, 1937; Brown and McGavin, 1982), although Lawton (1976) suspects that some species of *Chirosia* found on bracken likely have another major host. Studies of other fern genera are scanty, since most of the efforts on fern-arthropod inter-



Figs. 25–28. 25–26. Scanning electronmicrographs of *Chirosia betuleti,* third instar larva. 25, Posterior end of abdomen. 26, Posterior spiracles. 27–28. *Matteuccia struthiopteris.* 27, Close-up view of three galls caused by *Chirosia betuleti.* The pinnae are curled about the rachis of the frond (×0.8). 28, Fronds showing two types of galls: (C) gall caused by *Chirosia betuleti* characteristically placed in upper portion of the frond; (O) gall caused by *Olethreutes auricapitana* at the tip of the frond, which subsequently aborts (×0.12).

actions have concentrated on bracken for economic reasons. Monophagy does not appear to be the case for a number of *Chirosia* species since *C. parvicornis* is known from ferns of the genera *Asplenium, Dryopteris* and *Pteridium,* and *Chirosia hystricina* is known from ferns of the genera *Asplenium, Athyrium, Blechnum, Cystopteris, Dryopteris, Matteuccia, Osmunda, Polypodium,* and *Polystichum* (Wiezorek, 1973). The exclusive feeding on ferns by species of the genus *Chirosia* is an exception to the majority of fern feeding insects in which there is usually only one species of a genus that utilizes ferns as a food source (Hendrix, 1980). Indeed, if the conditions Hendrix (1980) poses for evidence of adaptive radiation, such as monophagous (or oligophagous) feeding by a closely related group of insects are correct, then the genus *Chirosia* ideally fits the mode. Biological studies of the remaining species are certainly necessary to support this speculation. It is also interesting that most of the *Chirosia*-fern associations are, with one exception (*C. hystricina* on *Osmunda*), found on modern polypodiaceous s.l. ferns.

The cover gall that *Chirosia betuleti* causes on either bracken or the ostrich fern differs with each host. In bracken, the gall is at the tip of the frond (Meijere, 1911), but in *Matteuccia* the gall is sub-apical. Unlike other types of *Chirosia* galls found on the unfurling frond tips, such as those caused by *C. albifrons* on bracken, or *C. parvicornis* on a variety of genera, the gall does not result in much damage to the tip of the frond as our results clearly indicate. The portions of the frond apical to the gall develop normally, with no significant decrease in height expansion of the leaf. The damage in the immediate vicinity of the gall remains localized and is not enough to disrupt transport systems within the affected fronds, which live as long as uninfested ones.

Chirosia betuleti was very specific in its feeding site. It seems from a count of eggs in newly emerged fronds that, initially, many more leaves had eggs than eventually developed galls. The larvae had to travel up the cleft of the adaxial side of the curled frond to arrive at the appropriate site, and failure to find the groove of the rachis or early disorientation probably proved fatal to the insects.

Although we did not carry out a detailed study concerning all predators on *Matteuccia* over the course of the season, it was readily apparent that very few were present at the beginning of the season. The only others we noted at that time were *Olethreutes auricapitana*, a lepidopteran that forms a gall within the last ten or so pinnae of the unfurling frond (this gall subsequently results in abortion of the leaf tip), and *Sparganothis reticulatana* Clemens, that caused localized disruption of the pinnae. Both of these species are polyphagous feeders and are not restricted to ferns. *Olethreutes* has been recorded from ferns by Ottosson and Anderson (1983) who found *O. lacunana* (Freeman) on pinnae of the bracken. Our records of *Sparganothis* apparently represent the first of this genus on fern.

Once the galls are vacated by *Chirosia betuleti*, they are taken over by the chloropid *Elachiptera costata*. This is the first report of *E. costata* and the first report of any chloropid known to occur on ferns (Hendrix, 1980). Previous available evidence suggested that the larvae of *Elachiptera* probably fed on decaying organic matter, such as old leaf sheaths, or decaying plant tissue and grass following damage by other insects (Sabrosky, 1948). *Elachiptera costata* was known previously to occur in rotting spathes of the aroid *Symplocarpus foetidus* (L.) Nutt. (Brown, 1956; Grimaldi and Jaenike, 1983). The distributions of the fern and aroid host plants do not overlap in Nova Scotia (Roland and Smith, 1969; Aderkas and Bird, 1983). In many other provinces and states the two do occur together in floodplains. Grimaldi and Jaenike (1983) suggest that most Diptera raised in their study of *Symplocarpus foetidus* probably also breed in decaying matter of other plant species, an observation that has been substantiated in the case of *Elachiptera costata*.

The appearance of eggs and larvae of *Chirosia betuleti* on unfurling fronds of the ostrich fern can be considered as possible food contaminants since the ostrich fern has long been utilized as a food plant in northeastern North America (Aderkas, 1983). We have observed eggs and larvae in both frozen and freshly picked fiddleheads sold in Nova Scotia. The frozen fiddleheads originated from New Brunswick, where these galls also have been seen in the field.

Table 1. List of Some Insects Collected in Association with the Ostrich Fern, *Matteuccia struthiopteris.*

Chirosia betuleti (Ringdahl) (Diptera: Anthomyiidae)—gall former on *M. struthiopteris.*
Elachiptera costata (Loew) (Diptera: Chloropidae)—secondary invader of galls.
Tricimba melancholica (Becker) (Diptera: Chloropidae)—probably secondary invader of galls.
Clinodiplosis sp. (Diptera: Cecidomyiidae)—secondary invader of galls.
Aphaereta n. sp. near *pallipes* (Say) (Hymenoptera: Braconidae)—Larval parasite of *Chirosia betuleti* (new species to be described by R. A. Wharton).
Elachertus loh Schauff (Hymenoptera: Eulophidae)—Larval parasite of *Chirosia betuleti.*
Dimmockia n. sp. (Hymenoptera: Eulophidae)—parasite, emerged from pupa of *Chirosia betuleti* (new species to be described by M. E. Schauff).
Olethreutes auricapitana (Walsingham) (Lepidoptera: Tortricidae)—gall former on *M. struthiopteris.*
Sparganothis reticulatana Clemens (Lepidoptera: Tortricidae)—feeding on *M. struthiopteris.*
Malacosoma disstria Hubner (Lepidoptera: Lasiocampidae)—pupating on fertile fronds of *M. struthiopteris.*
Lygus rubroclarus Knight (Heteroptera: Miridae)—commonly resting on *M. struthiopteris.*

Table 1 presents a list of the primary insects that were collected in association with the ostrich fern during our study. A number of various kinds of insects are casual visitors to this fern, but are not relevant to this study.

Acknowledgments

We are grateful to F. C. Thompson, C. W. Sabrosky, R. J. Gagne, P. M. Marsh, M. E. Schauff, D. C. Ferguson, and T. J. Henry, Systematic Entomology Laboratory, BBII, Agricultural Research Service, USDA, Washington, D.C.; V. Michelsen, Zoological Museum, Copenhagen, Denmark; R. A. Wharton, Department of Entomology, Texas A&M University, College Station, Texas; and P. T. Dang, Biosystematics Research Center, Agriculture Canada, Ottawa, Ontario, Canada, for identification or confirmation of various insects collected during this project. We are also grateful to H. J. Teskey, Biosystematics Research Center, Agriculture Canada, Ottawa, Ontario, Canada for reading the descriptions of the immature stages; and Karl Valley, Bureau of Plant Industry, Pennsylvania Department of Agriculture, Harrisburg, Pennsylvania, for reading the manuscript, for helpful and stimulating discussions during the preparation of the manuscript, and for providing the first instar larvae of *Macateeia protuberans.* We are also grateful to Mary Lou Cooley, staff artist, Systematic Entomology Laboratory, for her careful preparation of the fine larval illustrations, and P. Malikul, technician, Systematic Entomology Laboratory, for taking the SEM photomicrographs that accompany this paper. We gratefully acknowledge the field help of E. Butterworth, New Brunswick Research and Productivity Council, Fredericton, New Brunswick; J. Moore and P. Borwein, Dalhousie University, Halifax, Nova Scotia; as well as S. Johnson, N. Lewis and G. Williams, Atlantic Research Laboratory, Halifax, Nova Scotia. Help with statistical analysis by P. Green, Dalhousie University, Halifax, Nova Scotia, is acknowledged. Gratefully acknowledged is the support for a portion of this project that came through a Research Associateship awarded to the senior author at the laboratory of J. McLachlan, Atlantic Research Laboratory, Halifax, Nova Scotia. This paper represents NRCC publication no. 26322.

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